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Published in:
Animal

DOI:
10.1017/S1751731117003688
10.1017/S1751731117003688

Print publication: 01/01/2018

Document Version
Peer reviewed version

Link to publication

Citation for pulished version (APA):
Mrode, R., Tarekegn, GM., Mwacharo, JM., & Djikeng, A. (2018). Invited review: Genomic selection for small ruminants in Europe and other developed countries: How applicable for the rest of the world? *Animal*, *12*(7), 1333 - 1340. https://doi.org/10.1017/S1751731117003688, https://doi.org/10.1017/S1751731117003688

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Invited Review: Genomic selection for small ruminants in Europe and other developed countries: How applicable for the rest of the world?

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Abstract

Improved management and use of estimated breeding values in breeding programs, have resulted in rapid genetic progress for small ruminants (SR) in Europe and other developed countries. The development of SNP (single nucleotide polymorphisms) Chips opened opportunities for genomic selection (GS) in SR in these countries. Initially focused on production traits (growth and milk), GS has been extended to functional traits (reproductive performance, disease resistance and meat quality). The GS systems have been characterized by smaller reference populations compared with those of dairy cattle and consisting mostly of cross- or multi-breed populations. Molecular information has resulted in gains in accuracy of between 0.05 and 0.27 and proved useful in parentage verification and the identification of QTLs for economically important traits. Except for a few established breeds with some degree of infrastructure, the basic

building blocks to support conventional breeding programs in small holder systems are lacking in most developing countries. In these systems, molecular data could offer quick wins in undertaking parentage verification and genetic evaluations using **G** matrix, and determination of breed composition. The development of next-generation molecular tools has prompted investigations on genome-wide signatures of selection for mainly adaptive and reproduction traits in SR in developing countries. Here, the relevance of the developments and application of GS and other molecular tools in developed countries to developing countries context is examined. Worth noting is that in the latter, the application of GS in SR will not be a “one-size fits all” scenario. For breeds with some degree of conventional genetic improvement, classical GS may be feasible. In smallholder systems, where production is key, community based breeding programs can provide the framework to implement GS. However, in fragile growth systems, e.g. those found in marginal environments, innovative GS to maximize adaptive diversity will be required. A cost-benefit analysis should accompany any strategy of implementing GS in these systems.

Key words: Small ruminants, genomic selection, signatures of selection, QTL

Implication

The basic building blocks for conventional breeding programs for small ruminants in most developing countries are lacking. However, genomic data offers unique opportunities to circumvent some of the limitations through parent verification, genetic evaluations using the G matrix and understanding the molecular basis of adaptation

through GWAS. The application of genomic selection may however need to be tailored to the conditions of specific production environments e.g. smallholder verses pastoral systems.

Introduction: Role of small ruminants (SR) in developing countries

Globally, the largest number of SR occur in Asia (49.70%), followed by Africa (27.90%) and then Europe (8.70 %), summing up to 86.3% of world total (FAOSTAT 2013). SR meat and milk production represents 4.8% and 3.4% of the total meat and milk produced, respectively, in the world. These percentages are comparatively smaller in developed (3.0% and 1.6%) than in developing countries (6.2% and 6.1%, respectively), emphasizing the significant role of SR in developing countries. In addition, SR offer a wide range of products in developing countries including skins, manure and (mo)hair/pelts, and play critical socio-cultural roles in many communities (Kosgey and Okeyo, 2007). They also represent a large repository of genetic diversity that is well adapted to diverse agro-ecologies and are critical to the poor in marginal areas where arable agriculture is too risky or rearing cattle is not feasible (Devendra, 2002). The production systems in Europe are based mostly on improved management and well defined and structured breeding programs, while about 70 to 85% of SR products are derived from the smallholder and pastoral systems in developing countries. The smallholder and pastoral systems are low-input, characterized by small flock sizes, lack of infrastructure and animals of unimproved genotypes. Most often, higher productivity is not usually the goal trait, especially when production risks are high (Amer *et al.*, 1998).

Current advances in molecular biology has resulted in the discovery of unprecedented levels of genomic variation as a result of sequencing efforts, and consequently, the development of various single nucleotide polymorphisms (SNP) chips for genotyping purposes. The reduction in genotyping costs and advances in statistical methods (Meuwissen, *et al.*, 2001), has made it possible to incorporate molecular information in SR breeding programs in many European and developed countries to accelerate the rate of genetic progress in production and somewhat difficult to measure traits. The question that arises therefore is how applicable are the molecular based methods including genomic selection (GS) to the rest of the world especially in developing countries. This review presents an overview of GS and other molecular based methods in the improvement of SR in the developed countries and then examines their potential and feasibility for application in the developing countries.

Systems for conventional breeding programs in developed countries for SR

Fundamental to the implementation of GS is the existence of an already established system of genetic evaluation based on efficient performance and pedigree recording. In an attempt to increase the efficiency of the productivity of SR, many developed countries have implemented breeding programs based on estimated breeding values (EBVs) using performance and pedigree data. The maturity in mixed model approaches (Henderson, 1949) has resulted in more accurate estimates of EBVs accelerating the rate of genetic progress and the profitability of SR enterprises. For instance, in the New Zealand sheep industry there was an 83% increase in kg of lamb produced per ewe and

104 up to 28% overall in carcass weight from 1990 to 2012 (Beef and Lamb NZ, 2012).
105 Examples of established well-structured genetic evaluation systems that underpin such
106 genetic improvement programs for SR include Basco database for sheep and beef
107 improvement in the United Kingdom (http://www.basco.org/sheep), French genetics for
108 cattle, sheep and goats (http://en.france-genetique-elevage.org), Sheep Improvement
109 Limited - SIL in New Zealand (https://www.sil.co.nz/), and Canadian dairy goat breeding
110 program (http://www.goatgenetics.ca/).
111
112 These improvement programs for SR are mostly focused on meat, wool, and dairy
113 production, and more recently, breeding objectives have also included other functional
114 traits such as reproductive performance and disease resistance/tolerance but little
115 emphasis on carcass and meat quality traits (Pannier *et al.*, 2014). While rapid rates of
116 genetic progress for growth-related or milk traits have been achieved in these programs,
117 a relatively lower rate of progress is possible for traits that are measured later in the life
118 of females, such as reproductive ability, breeding seasonality and longevity (Rupp *et al*.,
119 2016) due to the longer generation interval or, in carcass composition traits which are
120 recorded on the relatives of selection candidates and require animals to be sacrificed
121 (Daetwyler *et al*., 2012).
122
123 **Overview of GS and molecular approaches in developed countries for SR**
124 The advent of GS and genome wide association studies (GWAS) opened new
125 opportunities for breeding programs in SR especially for traits measured late in life and
126 carcass traits. These opportunities in GS and GWAS resulted from the development of

next-generation sequencing technologies which allowed de novo sequencing of sheep and goat genomes; and the subsequent development of dense SNP Chips such as the Illumina Goat SNP50 BeadChip (Tosser-Klopp *et al.*, 2014), the Ovine SNP50 BeadChip (Kijas *et al.,* 2009) and recently the Ovine 600K SNP BeadChip (Anderson *et al*., 2014). Recently, a low density panel with 16301 SNPs for sheep has been developed by the International Sheep Genomics Consortium (Larroque *et al*., 2017)

The basic principle undergirding GS is that SNPs are assumed to be at LD with QTLs in the genome. Therefore the use of SNPs as markers enables all QTLs in the genome to be identified through the mapping of chromosome segments defined by adjacent SNPs. The implementation of GS usually involves estimating the SNP effects in a reference population which consists of individuals with phenotypic records and genotypes. This is then followed by prediction of genomic estimated breeding values (GEBV) for selection candidates with no phenotypes of their own (Meuwissen, *et al.*, 2001). Details of the design of actual GS in SR have been described by Rupp *et al*. (2016).

Genomic predictions and selection in SR for developed countries have either been successfully implemented or their feasibility demonstrated on a number of standard production traits such as wool, growth traits, muscle and fat depth in New Zealand (Auvray *et al.*, 2014), Australia (Daetwyler *et al*., 2010), in dairy sheep and goats in France (Carillier *et al*., 2014) and in dairy goats in the UK (Mucha *et al.,* 2015). Recently GS in SR has been applied to breed for disease resistance such as parasite and fly-strike resistance (Pickering *et al*., 2015) and facial eczema (Phua *et al*., 2014). There is

also on-going work on genomic prediction for traits such as feeding efficiency and methane emissions (Pickering *et al*., 2015).

The characteristics of these genomic prediction systems for SR include reference populations of smaller sizes compared to dairy cattle and consisting of mostly cross-breeds or multi-breed populations. In summary, the reference populations ranged from 1,900 for Western Pyrenees dairy sheep breeds to 8,000 multi-breed Australian meat sheep (Rupp *et al*, 2016). The gains in accuracy provided by molecular information are rather lower (range from 0.05 to 0.27) given the small size of the reference populations. Details of accuracies from studies on genomic predictions for SR are outlined by Rupp, *et al*. (2016).

Genomics has offered the opportunity to identify and include major genes (QTLs) associated with reproductive, disease, or production traits. A comprehensive list of such QTLs is outlined by Rupp, *et al.* (2016) including some of the genes that are already being used in breeding programs, such as *PrP*, *FecL* or the *α-s1* casein (French goats), to pre-select candidates for progeny testing. In recent times, genomic approaches have been used to identify novel mutations influencing functional traits. For instance, Demars *et al*. (2013) used GWAS and identified new mutations associated with prolificacy in sheep. The discovery of actual genes and causative mutations underlying prolificacy has been a subject of intense investigation in sheep in developed countries. The findings have paved the way for the development of commercial DNA assays/tests/Kits, which require no parental information, to identify breeding stock with high prolificacy.

Such tests have been developed for the Inverdale (*FecX*^{I}) and Boorola (*FecB*^{B}) mutations and are commercially available in Australian and New Zealand sheep industry where rams are tested to breed heterozygous progenies (Davis 2005; Walkden-Brown *et al*. 2009).

In addition to genomic prediction, the use of genotypic information plays an important role in parentage verification and assignment in SR in developed countries. In breeding schemes for SR, parentage identification is an issue due to the limited use of artificial insemination and use of natural mating, involving most likely multiple sires, in extensive systems. In these natural mating schemes parentage is either unknown or incomplete and the use of genetic markers, initially microsatellites and currently SNPs, have proved useful to detect misidentified and unknown parents. For details of the various SNP chips available for parentage verification, the reader should see Rupp *et al.* (2016). In addition to parentage identification, genotypic information is useful for assessing genetic diversity and structure of local sheep and goat breeds. Genotypic data gives more accurate estimates of relationship between individuals than pedigree records and therefore offers better opportunities for more accurate estimation of co-ancestry, mate assignment, and inbreeding coefficients (Rupp *et al*. (2016).

Summary of some breed improvement programs for SR in developing countries

The existence of well-established conventional genetic evaluation and selection programs provide the necessary platform for the implementation of GS. In most developing countries, genetic improvement programs for SR are scarce. The major

constraints include lack of performance and pedigree information and the non-existence of institutional frameworks and infrastructure including inadequate farmers' organizations at the village level to effectively participate in breeding schemes (Kosgey and Okeyo, 2007). Most of the production occurs in small holder systems which are characterized by small flock sizes, uncontrolled mating and lack of pedigree recording and therefore the difficulty of defining adequate contemporary groups. However in a few countries, breeding improvement programs for SR have been implemented, and these are briefly summarized.

(i) Kenya Dual Purpose Goat Development (KDPG) Project

The KDPG breeding program was started in 1980 as part of the Small-Ruminant Collaborative Research Support Program (SR-CRSP) funded by the United States Agency for International Development (USAID) and implemented by Kenya's Ministry of Livestock Development. The overall objective was to develop a synthetic breed of goat that combined the adaptability of the indigenous East African and Galla goats and the growth and milk producing abilities of theToggenburg and Anglo-Nubian breeds. Ojango et al (2010) provides a detailed summary of the breeding program for the KDGP goat.

The foundation flock consisted of 250 Small East African (E) goats from across Kenya and 200 Galla (G) goats sourced from the dry Northeastern province of Kenya. With no production data available, these animals were selected based on phenotypic characteristics such as large and sound udders and teats and the local "milk line" claim, a distinctive black stripe along the back of some Galla goats. These were initially mated

to different Toggenburg and Anglo-Nubian bucks, and later insemination was done using semen from the USA. A nucleus breed was established at Ol-Magogo Estate of the National Animal Research Centre, Naivasha (Mwandotto *et al*. 1992), where productivity and pedigree recording was undertaken by enumerators. An interdisciplinary farming systems approach was used (Ojango *et al*. 2010) to develop and test the breeding program (Semenye *et al*. 1989). KDPG development occurred at Ol-Magogo Estate, while breeding animals were provided to a station in Maseno Western Kenya, which was closer to the target farmers. On-farm testing of the KDPG was carried out by smallholder farmers from contrasting socio-cultural and environmental backgrounds. Each farmer received 2-4 breeding does and breeding bucks were rotated amongst groups of farmers. The project developed the KDPG breed. On-farm the KDGP reached their milk peak after one week of kidding, producing 600ml per day for household use while On-station, it reached peak milk production, three weeks after kidding, producing 1500ml per day (Onim 1992). In on-farm trials, the KDPG produced on average 0.49 litres per day with a range of between 0.05 and 2.70 litres per day (Semenye *et al*.,1989). The local does at the station peaked after six weeks of kidding, producing a daily milk production of 400 ml (Onim 1992). At the peak of its operation, a breeding flock of the KDPG established at Ol-Magogo Estate stood at 1800 animals. By 2005, the population was less than 400 animals (Bett, 2005) due to the termination of the breeding and farmer development program for the KDPG and the SR-CRSP project (Ojango *et al*. 2010). Within the last decade, there has been renewed interest in the KDPG and a re-evaluation of its breeding strategies (Ojango *et al*., 2010).

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243

244 *(ii) Community Based Breeding Programs (CBBPs) for Sheep and goats in Ethiopia*

245 The International Center for Agricultural Research in the Dry Areas (ICARDA), the
246 International Livestock Research Institute (ILRI), and Austria's University of Natural
247 Resources and Life Sciences, in partnership with the Ethiopian National Agricultural
248 Research System (ENARS), have designed and implemented community-based SR
249 breeding programs in Ethiopia since 2009 (Haile *et al*., 2014). Similar CBBP for
250 indigenous goats of Ethiopia and Cameroon were also implemented by Biosciences
251 Eastern and Central Africa (BecA-ILRI) Hub in 2013 for three production systems (arid
252 agro-pastoral, semi-arid agro-pastoral and highland mixed crop-livestock systems;
253 Woldu *et al*., 2016). The CBBP are designed to take into account farmers' needs, views,
254 decisions, and active participation, from inception to implementation, and their success
255 is based upon proper consideration of farmers' breeding objectives, infrastructure,
256 participation, and ownership (Wurzinger *et al*. 2011). The goal of CBBPs is to improve
257 the productivity and income of small-scale resource-poor SR producers by providing
258 access to improved animals that respond to improved feeding and management, and
259 facilitating the targeting of specific market opportunities.

260

261 There is a governmental rural organization associated with each of the sites where the
262 CBBPs are in operation. Local enumerators are recruited for each site to assist the
263 research system in animal identification and recording. Indigenous knowledge of the
264 community is considered at each phase of the project. For example, the community

decides how rams are managed and how they are shared and used. The aim is to get community members to work as a team in selecting, managing and using rams. Two stages of selection are applied, initial screening when first sales of young rams occur (4–6 months) and final selection for admission to breeding at 12 months of age. Selection at the first stage is based on 6 months weight and ewe lambing interval. Yearling weights and body conformation are considered in the final selection.

There are currently 23 CBBPs across Ethiopia operating in 15 sheep and 8 goat sites. Each CBBP involves an average of 60 households per site and 600 flocks with an average flock size of 10 animals. To automate the recording and ensure real-time archiving, an online database “DREMS” (Data Recording and Management System) was developed (jointly by EMBRAPPA-Brazil and ICARDA). In DREMS, data can be keyed-in offline from a mobile devise (tablet, computer, mobile phone etc.) and updated once online. The information is archived in a server maintained at EMBRAPPA-Brazil.

(iii) Goat improvement programs in South Africa

The South Africa Boer Goat Breeders’ Association was formed in 1959 but development of the Boer goat as a meat breed dates back to 1918. The National Performance Testing Scheme however, commenced in 1970. Two other dairy breeds were further developed from the Boer goat. These were the White Savanna, which was initiated in 1957 and a breed society formed in 1993 and the Kalahari Red which started in 1990. Genetic improvement of these dairy goats is still based on the convectional hand and eye method (Casey and Webb, 2010) and the South African Studbook Association and

Milch Goat Breeders Society handles records of goat breeds and milk production. Genetic progress is rather slow, but substantial amount of genetic improvement has been realized in the past especially in the meat goat sector.

Animal recording in the mohair producing Angora goats, was piloted in 1983, with the approval of the Angora Stud Breeders' Society. This was followed by the closure of the Angora herd book in 1984 and in 1999 animal recording for the Angora goat was operationalized within the National Small Stock Information Scheme of South Africa. The breeding program for the Angora goat in the South African mohair production systems was designed on the basis of the study by Snyman and Olivier (1999). The initial selection index was based on fibre diameter, fleece weight and body weight. Intensive selection for increased mohair production from the early 1970s until 1990 with no selection directed towards weaning weight, resulted in unthrifty animals with an inability to survive sub-optimal conditions (Visser and Van Marle Köster, 2014). The selection strategy was re-evaluated in 2002 and it was concluded that selection for decreased fibre diameter, while maintaining or increasing body weight and fleece weight seems optimum for the breed. In addition, molecular research has been undertaken with a view of including molecular information in the breeding program. A microsatellite marker panel consisting of 14 markers has been developed and utilized for parentage verification in the Breed (Visser *et al*., 2011a). Similarly eighteen QTLs for mohair traits including fleece weight, fibre diameter and other related traits have been identified on thirteen chromosomes (Visser *et al*., 2011b).

(iv) Goat and Sheep improvement programs in India

A goat improvement program involving 34 villages was initiated by the Nimbkar Agricultural Research Institute in 1991 in South-Central Maharashtra of India with the aim of improving goat productivity through cross-breeding (Nimbka, 1991). Thirty-four villages within a 15 km radius of Phaltan town in South-Ccentral Maharashtra province formed the target area for the cross-breeding project. It involved 13 Sirohi bucks selected on their individual growth rates and their mothers' milk yields, ten Alpine x Sirohi and ten Toggenburg x Sirohi bucks which were bought and introduced into the project. The improved bucks were placed in the villages for cross-breeding of local goats and no efforts were made for the dissemination of cross-bred males and females generated in the course of the project. The project was supported by veterinarians, who visited each project village once a week. The project ran for four years but collapsed due to lack of funds. The author concluded that it provided a framework for an effective breeding program when individual units are small and spread out over a large area. Similar cross breeding program to improve the fecundity of Deccani sheep of Maharashtra was summarized by Nimbka *et al*., (2002), which involved the introgression of the Booroola gene from the Indian Garole breed into the Deccani and a composite breed.

The relevance of developments in GS and other molecular approaches in developed countries for the rest of the world

Parentage and breed composition verification

One the possible quick wins from the developments in molecular based approaches and the utilization of genotypic information in SR breeding in developing countries includes

parent verification and breed composition of cross bred animals. The rather extensive systems for the management of SR in small holder systems and the lack of infrastructure to capture pedigree information has resulted in the inability to undertake genetic evaluation in these systems or control breeding. Therefore the availability of genotypic information will reduce the need for accurate pedigree recording as genomic relationships can be computed to undertake genetic evaluation, estimate inbreeding and undertake parentage verification. However most of the initial work on parentage verification so far in these systems are based on microsatellites. A microsatellite marker panel consisting of 14 markers has been developed and utilized for parentage verification in the Angora Breed (Visser *et al*., 2011a). Similarly, genotypic data can easily be used through admixture analysis to determine breed composition in cases where crossbreeding and uncontrolled mating is practiced and therefore be utilized to match appropriate genotypes to the relevant management systems. However the utilization of genomic information in the small holder systems for SR is rather slow compared to dairy cattle where genetic predictions have been undertaken using the **G** matrix computed using SNP data (Brown *et al.* 2016). In the ILRI led Africa Dairy Genetic Gains (ADGG) project, a small chip of about 400 SNPs for parentage verification and breed composition for dairy cattle is being developed (Gibson & Mwai, personal communication).

Detection of signatures of selection and use of molecular markers in breeding in small ruminants

In contrast to SR in Europe and the developed world, SR in the developing countries remain nondescript in genotype and phenotype, the consequence of modest anthropological selection. The analysis of microsatellites and recently SNP genotype and full genome sequence data in SR in the developing world has revealed high genetic diversity that mirrors their extensive phenotypic diversity as well as the diversity in their production environments and historical migration and admixture patterns. Analysis of signatures of selection have revealed candidate regions in the genome harbouring genes with demonstrated roles in phenotypic variation including fat and thin tail, horn size and polledness, body morphology, limbs and skeleton development, pigmentation etc. (Fariello *et al*., 2014). In a GWAS study, Gholizadeh *et al.* (2015) identified significant association between a single SNP located in the *SYNE1* gene on chromosome 8 with yearling weight in Baluchi sheep found across southwest Pakistan, eastern Iran and southern Afghanistan. Using different approaches, multiple selection sweep regions spanning several candidate genes relating to various traits (immunity, nervous and endocrine system development, metabolism, thermo-regulation, reproduction etc.), metabolic pathways and biological processes driving adaptation to local environments have been revealed in Black, Draa and Northern goat populations of Morocco (Benjelloun *et al*., 2015), various breeds of sheep in Africa, Asia and South West Asia (Fariello *et al*., 2014), Barki sheep and goats from Egypt (Kim *et al.,* 2016) and the indigenous goats in South Africa (Mdladla, 2016). Kim *et al.* (2016) further identified one selection sweep region that was common to both the Barki sheep and goats from Egypt providing possible evidence for a common region under selection in a common environment in the two species. Gouveia *et al*.(2017) identified genomic

regions under selection which overlap genes influencing traits associated with ecological adaptation, phenotypic and production differences amongst three Brazilian locally adapted sheep breeds (Brazilian Creole, Morada Nova and Santa Ines). It is worth noting that in most of these studies, the identified selection sweeps and their genomic distribution differ between populations/breeds but reflect, to a large extent, the outcomes of local adaptation. This suggests that artificial selection seems to play a minor role in driving genome evolution in SR in developing countries and natural selection tends to favour adaptive diversity.

The characterization of the indigenous goats in Ethiopia and Cameroon populations using mitochondrial DNA and 50k SNP chip array was also undertaken by Getinet, (2016). A high level of genetic diversity but weak genetic structure was found among the goat populations in both countries. However, the Keffa goat, reared in highly tsetse infested area, and Abergelle goat, also known with its drought tolerance, were found to have relatively maintained their pure genetic background. Coding regions of the kisspeptein gene were found in Gondar and Woyto-Guji goats in Ethiopia and the genotypes detected were associated with multiple births in these goat populations (Getinet *et al*., 2016).

With the exception of Brazil and possibly India, the use of molecular markers in SR breeding lags behind in most developing countries. In Brazil use of molecular markers in animal breeding has concentrated on two fronts: those controlled by many genes of small effect (meat and milk production, Lôboa, *et al*., 2010), on which classical

breeding is based, or traits controlled by few genes of large effect. The latter have several examples in sheep such as those linked to prolificacy (booroola, inverdale or galway), muscle mass (callipyge) or resistance/susceptibility to scrapie (PNRP). Castro *et al*. (2006) identified a mutation linked to prolificacy specific to naturalized Brazilian breeds.

Potential for the application of genomic selection in developing countries

The production system for SR in developing countries can be considered to occur along a trajectory in terms of management systems with one end of the spectrum consisting of breeds operating mostly on a commercial scale basis, having some degree of genetic improvement and investment on infrastructure while on the end is the fragile growth systems, mostly the pastoralists/nomads in arid environments. (Smith, *et al*., 2013). Opportunities for the application of GS will therefore not be ”one size fits all” but very much dependent on the intersection of the spectrum being considered. Commencing at one end of the spectrum where production is at a commercial scale, with some organizational structures (breed societies) and some investments in IT infrastructure, such as the Boer, Savanna, Kalahari and Angora goat breeds in South Africa, huge opportunities exist for GS. In this production system, the emphasis is mostly on productivity traits with less weight put on adaptive traits. The existing structures such as the progeny testing scheme (Snyman and Olivier, 1999), the availability of performance and pedigree records imply that classic GS (GBLUP or Single step) could be applied. Potential improvements in this setting is to translate to the use of digital systems (mobile phones or tablets) to collect performance data (Mrode *et. al*., 2017), as it avoids or

reduces the huge organizational infrastructure and high costs associated with recording systems. Additional benefit from genomics in this setting is the reduction for the need to accurately record pedigrees as genomic relationships can be computed and parentage verification implemented using SNP genotype data.

In the middle of the spectrum are the small holder systems which account for most (70-80%) of the outputs from SR. While the emphasis here is still on production traits, adaptive traits play very significant role, therefore innovative GS will be needed that ensures adequate balance between production and adaptive traits. However, community based breeding programs, such as the FARM-Africa Meru and Tharaka-Nithi Districts dairy goat and animal healthcare project in Kenya among other initiatives, seem to be the best approaches for implementing GS as the rotational use of selected males provide opportunity to select superior males using SNP genotype data, given that performance recording pooled from several flocks by digital means can be initiated or is already in place. The within breed selection implemented in these projects ensures that adaptability of local breeds can be monitored overtime and mating can be controlled. However several scenarios need to be evaluated considering different genotyping strategies and the economic aspects to determine the best approach for implementing GS in this setting. In addition, production and adaptive traits can be optimized in the context of CBBP via gene/genome/haplotype block editing (Jenko *et al*., 2015) utilizing the genomic regions identified in combination with GS in developing appropriate synthetic breeds.

At the other end of the spectrum is the fragile growth systems consisting mostly of very extensive systems of the pastoralists and nomads in arid and semi-arid environments, where adaptive traits are key and the main goal will be to maximize adaptive diversity. The implementation of GS in this system possess major challenges. However the widespread usage of the mobile phone in these systems for other purposes, such as money transfers, imply that digital data capture and recording could be possible with adequate farmer training. The use of communal grazing lands, watering points and other services could innovatively be used to introduce recording of basic performance data, initiate sampling for genotyping of animals and also introduce the use of superior males. The initial use of such data could be the application of GWAS and investigating signatures of selection to identify genomic regions associated with various aspects of adaptability (disease and drought for instance). As more data accumulates, genomic data will allow for a better understanding of genetic diversity in the fragile growth sector and how to select for it: for instance, the use of weighted GBLUP or Bayesian methods to optimize various aspects of adaptability. In the long term, usage of gene editing in addition to GS to increase and optimize the frequency of favourable alleles associated with different aspects of adaptability (Jenko *et al*., 2015) could be a possibility.

Economic aspects of genomic selection in developing countries

Given the significant role that SR play in the livelihood of farmers, the implementation of GS in the various management systems described especially the low-input small holder system and the fragile growth sectors should be accompanied by a cost-benefit

analysis. The bottom line is that the introduction of GS should financially be beneficial to farmers and produce animals that are able to fulfil the other socio-cultural roles played by SR in the community. The relatively high economic efficiency of GS in the dairy cattle is derived mostly from the large reduction in generation interval (König et al 2008). In small ruminants, the reduction in generation interval is not as large (Larroque et al, 2017) and the relatively higher cost of genotyping limits the cost-effectiveness of GS. Shumbusho et al (2016) found that GS alone was not more beneficial in a French meat sheep breed compared with classical selection except when compared with some early measured phenotypes. However the introduction of the low density chip (16k) for sheep increases the prospects of higher economic returns from GS. Larroque *et al*.,(2017) demonstrated very high accuracy of imputation of the 16K chip to the 50k Chip and concluded that it increases the cost-effectiveness of genomic selection for French sheep breeds. Prior to implementing GS, some aspects to consider include product management and marketing issues that may accompany improved productivity and the prevailing socio-economic status of farmers, and flock structures and dynamics within the smallholder system. However cost can be reduced by sharing facilities such as databases or analytic platforms which may already be in existence for other livestock species such as cattle. The availability of the LD chip for sheep increases the prospect of long term genomic selection in small ruminants in developing countries.

Conclusions

Unique genotypes of several goat and sheep breeds found in developing countries and especially in Africa present a good opportunity for understanding genetic diversity,

494 structure and adaptation. The availability of molecular tools and approaches have
495 enabled the understanding of the genetic basis for this diversity and adaptation, initially
496 through the use of microsatellites and more recently SNP genotype and full genome
497 sequence data. This information is foundational in terms of its incorporation in future
498 breeding programs for SR in developing countries. In the long term, the use of
499 gene/haplotype editing and other emerging breeding strategies could play a role in
500 incorporating these into breeding programs for increased productivity.
501
502 The basic building blocks for conventional breeding are lacking in most of the small
503 holder systems in developing countries apart from a few of the established breeds with
504 some degree of supporting infrastructure. Genotypic data offers quick wins in terms of
505 parentage verification, breed composition determination (admixture) and genetic
506 evaluation using the **G** matrix.
507
508 Genomic selection in SR in developing countries will not be a scenario of “one-size fits
509 all” but it will depend on the type of production system. Classic GS is feasible in breeds
510 with some degree of conventional genetic improvement already in place. The CBBP
511 provides a good framework for the implementation of GS in small holder systems and
512 Innovative GS will be needed in fragile growth systems where adaptation is an
513 important trait. Identifying regions of the genome associated with various aspects of
514 adaptability and maximizing diversity of adaptation in animals reared will be essential.
515 Adequate cost-benefit analysis should be part of any strategy adopted in implementing
516 GS in these production systems.

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